The Effects of Mating on Predation in the Stick Insect *Diapheromera veliei* Walsh (Phasmatodea: Heteronemiidae)[1]

JOHN SIVINSKI

Department of Biology, Univeristy of New Mexico, Albuquerque, New Mexico[2]

ABSTRACT

Diapheromera veliei Walsh engage in lengthy pairings (3–136 hours). Mating may increase or diminish the danger of predation, depending on whether individual defenses are inhibited or pooled. The relation between mating and mortality has not been previously quantified in any animal. *D. veliei's* defenses are cryptic coloration and posture, regurgitation, and reflex bleeding. When mating pairs and single individuals were exposed to Mexican jays, females had significantly greater survivorship when mating. There was no difference between mating and single male mortality. It is argued that females do not directly determine coupling duration and that increased protection is an effect and not the function of extended mating.

Sex often imposes risk (Daly 1978). Chemical, bioluminescent, and acoustic signals emitted in the context of reproduction are exploited by predators and parasitoids (Walker 1964, Mitchell and Mau 1971, Lloyd 1973, Cade 1975, Mangold 1978). Exposure while searching for mates can result in greater male mortality (see Edmunds 1976, Downs 1978). The act of insemination may decrease monitoring of the environment by burdening the nervous system (Jackson 1976). Pairing frequently entails disruption of cryptic postures and may inhibit escape reactions.

Paradoxically, some individuals spend large proportions of their lives in seemingly vulnerable reproductive positions. *Diapheromera veliei* Walsh (Phasmatodea: Heteronemiidae) mates from 3–136 hours in the laboratory and other stick insects cleave together for weeks or months (Gangrade 1963, Gustafson 1966). Mate guarding is the most common interpretation of such major time investments by males (Parker 1974). By blocking access to the female genitalia, a consort forestalls sperm competition (Parker 1970). A greater loss of fitness may result from introduction of a rival ejaculate than from an increased chance of mortality due to coupling.

Under certain conditions, however, pairing could serve as a defensive alliance (Chaplin 1973). Arthropods often possess elaborate chemical and physical defenses (Eisner 1970). Close proximity enhances certain predator deterrents (intensity of aposematic signals, Cott 1957; snapping jaws in owlfly larvae, Henry 1972; sticky exudate in sawfly larvae, Tostowaryk 1972). Eisner (1965) suggested that the pooled chemical defenses of a coupled male and female might be an adaptive justification for the long matings (up to 3 weeks) of the phasmid *Anisomorpha buprestoides* (Stoll).

Copulation may expose or shelter its participants, depending on their defenses and the predators encountered. This paper examines the possibility of predation influencing the sexual behavior of *D. veliei*.

Methods

Adult *D. veliei* were obtained in Bernalillo and Sandoval Counties, New Mexico, from the shrubby legume *Dalea scoparia* Gray. The mobility and crypticity of mating pairs and single individuals were estimated and the defenses of both sexes examined. Feeding trials using captive birds were made to determine differential mortalities.

Comparisons of crypticity were accomplished by placing a male, a female, and a mating pair on one side of a *D. scoparia* bush. Human observers (n = 24), viewing from a distance of 10 feet, marked the positions of insects and their order of discovery on a drawing of the bush. Movement was noted. Because any activity greatly increased conspicuousness, such observations were discarded.

To observe reactions to initial contact with a predator, phasmids in the field were tapped on the abdomen with a pencil. Their response was quantified on a scale of 0 to 3 (0, no reaction; 1, a withdrawal <15 cm; 2, a short dash <30 cm; and 3 a long dash >30 cm often accompanied by a drop through the foliage). Observations were made of 88 single males, 14 single females, 22 mating males and 29 mating females. Defenses other than active escape (regurgitation, reflex bleeding, body movements) were elicited by squeezing the thorax; 110 males and 43 females were examined.

The palatability of regurgitants was tested by simultaneously offering 3 mealworms covered with crop contents and 3 untreated mealworms to 5 insectivorous rodents (*Onychomys leucogaster* (WiedNeuwied)). Sugar solutions with and without crop contents were presented to 30 ants (*Pogonomyrmex rugosus* Emery) contained in a small aquarium. Activity (recruitment feeding) at the two solutions was recorded over time. Hemolymph was obtained by puncture and presented to ants in the same manner as crop contents.

A *D. scoparia* bush with a wooden cross perch arranged in its center was placed within a large enclosure containing two Mexican jays (*Aphelocoma ultramarina* (Ridgeway)). Insects were placed on the bush and predation observed from a blind for periods of various duration for 14 days. An individual was scored as surviving if a bird dropped it, did not immediately return, and

the insect was capable of locomotion. The longterm effects of damage inflicted during abandoned attacks are unknown. Many insects were apparently unharmed.

O. leucogaster, P. rugosus, and *A. ultramarina* are sympatric with *D. veliei* over parts of its range and may prey on it or be representative of its natural predators.

Results

Robinson (1969a) divided insect defenses into primary defenses which reduce the probability of detection, and secondary defenses which discourage predation following discovery. The primary defenses of *D. veliei* are, as in most Phasmatodea, special protective resemblance to vegetation and behaviors (swaying and leg postures) that enhance this mimicry.

Mating pairs, single males, and single females did not differ significantly in crypticity to human observers (of 21 observers, 5 first noticed a single male, 7 a single female, 9 a mating pair: $0.50 > p > 0.25$). This result, while suggestive, is of questionable applicability to *D. veliei* in nature, because human visual acuity may differ from that of key predators.

Coupling hampered response to disturbances only of males. Mating males moved less than single males ($\bar{x}$ mating $= 1.0$, $\bar{x}$ single $= 1.75$, chi square test $p < 0.001$). Mating and single females did not differ in their reaction to a pencil tap on the abdomen ($\bar{x}$ mating $= 0.758$, $\bar{x}$ single $= 0.818$, chi square test $p > 0.10$).

When handled, these insects assume either a rigid, motionless posture with legs extended or a limp death-feigning attitude, or alternately grip and flail with the legs. *D. veliei* bears subproximal spines on the mid and hind femora. These spines are enlarged and hooked on the mid femora of males. If these projections serve an antipredator function, better-endowed males might react with agitation to grasping more frequently than females. When handled, 0.57 of 110 males and 0.47 of 43 females displayed agitation. There was no difference in their behavior (chi square test $0.25 > p > 0.10$). Spines may aid in clasping stems, making it difficult to remove the insects from plants. Male-male aggression, common in *D. veliei,* probably accounts for the sexual dimorphism in armature (Sivinski 1978).

Walkingsticks lose limbs easily. A jay was observed to strike at a phasmid and remove a leg. A sizable proportion of *D. veliei* sampled (0.18 of 43 adult females and 0.25 of 110 adult males) lacked one or more legs. These might have been lost to predators or dropped during molting as in the related *Diapheromera femorata* (Say) (Severin 1911).

D. veliei regurgitates when captured. Mantids, jays, and primates have observed gutting and discarding the crops of orthopteroid insects prior to consumption (Robinson 1969b, Eisner 1970, Edmunds 1974). Some grasshopper regurgitants repel ants (Eisner 1970). Of 10 adult *D. veliei* presented to the insectivorous rodent *O. leucogaster,* 3 had large portions of the gut removed and discarded. Two were females whose rejected portions of digestive tract measured 20 and 27 mm. The much narrower male crop was 10 mm. Female regurgitants tended to be of a larger volume, and females are more apt to vomit when handled (0.72 of 43 females, 0.34 of 110 males, contingency chi square test, $p <$

0.001). This difference may reflect a greater defensive potency of the female regurgitant due to its quantity.

Mealworms mixed with *D. veliei* gut content were less palatable to *O. leucogaster* than untreated worms. Fifteen control mealworms were consumed; none was rejected. Eight of 15 treated worms were eaten, but only after the clean larvae were gone (Fisher test, $p < 0.01$). Ninety-seven ants visited an unadulterated sugar solution over a period of 70 minutes, opposed to 11 at the sugar/gut content solution (t-test, $p < 0.001$).

Yellow fluid (identical in color and viscosity to hemolymph) occasionally appears along the integumental sutures of *D. veliei* when handled. The only previous report of reflex bleeding in the Phasmatodea is of certain species of *Bacillus,* whose blood flows from the membrane joining the abdominal tergites under poorly determined conditions (Chopard 1938). Droplets arise from between all thoracic and most abdominal segments, the coxal areas, and tarsi. Volume varies; the greatest occurs on the female abdomen, the smallest between the tarsi. The latter can be smeared on an attacker by leg movements. Physical damage (e.g., a bird peck) results in a similar flow. Of 143 individuals examined, 23 reflex-bled. Males were more apt to bleed than females (20 of 110 males, 3 of 43 females). No ants visited a sugar and blood solution over a period of 245 minutes compared to 51 visits at the control (t-test, $0.005 > p > 0.0025$).

A female *D. veliei* tethered near an ant nest (*P. rugosus*) bled from wounds near the coxae. When an ant encountered blood it dropped from the phasmid and cleaned its mandibles in the soil or with its forelegs. A male staked by the same colony reflex-bled from the base of the left midleg. This area was inspected and then avoided by several ants. Both individuals were dead and partially dismembered in 20 minutes, but had escape been possible and attackers less numerous, bleeding might have been an effective defense.

The results of feeding trials using jays as predators are shown in Table 1. Of 46 single individuals, 14 (30%) survived (i.e., were discarded while alive and capable of walking) with no difference between males (38%) and females (24%) (chi-square test, $0.25 > p > 0.10$). Nearly 67% of mating insects survived, a significant difference compared with single adults (chi-square test, $0.005 > p > 0.001$). The 22% increase in male survivorship when mating is not a significant change over single male mortality (chi-square test, $p > 0.10$). The bulk of the difference between single and mating insect survivorship is due to the substantial decrease (49%) in female mortality ($0.0005 > p > 0.001$).

Discussion

Several factors might account for the higher survival of copulating females. The summed chemical defenses of mating *D. veliei* may be more potent. Droplets of blood and regurgitant are localized on the body surface and the probability a predator will come into contact with them might be greater as they become more numerous. *D. veliei* is a large insect ($\bar{x}$ male length from head to abdominal tip $= 74$ mm, $\bar{x}$ female $= 80$ mm). Mating pairs usually stay together for some time after being picked up, particularly if the female alone is held

Table 1.—The outcomes of bird attacks on single and mating *D. veliei.*

	Number attacked	Number surviving[1]	Percent surviving
Males			
Single	21	8	38
Mating	15	9	60
Females			
Single	25	6	24
Mating	15	11	73

[1] Surviving initial attack (see text).

in the bill. They might constitute an unwieldy object for many predators. Opportunities for the insect's escape while in transit to or at a feeding site might be increased by the divided attention of a predator simultaneously confronted with 2 individuals. Mating males may suffer higher mortality than females because of their vulnerable dorsal position *in copulo.*

There is a difficulty in ascribing the function of extensive coupling to defense: males have direct control of mating duration and even if male survivorship is enhanced, survival is not synonymous with reproductive success. Male fitness would not be increased by maximizing life span at the expense of reducing the number of mates he might encounter. Under the following circumstances, however, increased male time investments could evolve in the context of predation, either by benefiting the male or by manipulation of males by females who benefit from their presence.

1) Searching while mating: In *D. veliei*, the mobility of mating males during escape is approximately half that of single males. The overall mobility of coupled males is probably lower as well. If attached males encounter females at less than the normal rate, then increased search time due to escape from predation (I) would have to be greater than the reciprocal of the lower rate (r) for mating extension to be adaptive ($I > 1/r$). Male *D. veliei* do not foil predators by remaining in copulation.

2) Protection of future offspring: Guarding females against predators is adaptive when single female mortality is so high that, by abandoning a mate, a male loses reproductive success even if subsequent females are found and inseminated.

Female *D. veliei* are considerably bulkier than males (ca. 3 times as heavy), which might discourage or attract various predators. The tachinid parasitoid *Thrixion halidayanum* Rord., for instance, attacks only female phasmids (Clausen 1940). Field surveys before and after the peak nesting season of arid grassland birds show that sex ratios of the phasmids change from near parity to a male bias of 4:1. Late instar nymphal sex ratios for much of this time were not significantly different from 1:1 and female numbers fall, making it unlikely that sexual dimorphism in maturation alone can account for this difference (Sivinski 1977). Adult females are polychromatic, with 4 color morphs. Male colorations differ by shading of similar hues. Polymorphism can be due to selection exerted by search-image-forming predators (Clark 1962). The data are insufficient for speculation on whether predation is severe enough to select for male guarding.

3) Manipulation by females: Female mobility and detectability were little changed by mating, and survivorship increased dramatically. If males monitor the progress of insemination, they may be vulnerable to female manipulation. For example, females accepting ejaculates at a slower rate might result in males remaining *in copulo* for longer periods of time. In *D. veliei* the penis is periodically inserted into the vagina where it remains during ca. 60% of the coupling. In extended matings of other phasmids, intromission is followed by long periods during which the genitalia are not in contact and insemination is apparently completed (Le Feuvre 1939, Hetrick 1949, Gustafson 1966).

The correlation among phasmids between extensive mating and defense is made tenuous by the number and phylogenetic range of species engaging in lengthy copulations (le Feuvre 1939, Korbott 1961, Gangrade 1963, Gustafson 1966, Clark 1974). Defensive capabilities, size, and predators encountered are unlikely to be equivalent in all cases (see Bedford 1978). The apparently pseudosexual relations between nymphs of the stick insect *Anisomorpha buprestoides* may be defense cooperatives (Eisner 1965). Sequestering of future mates by males could also account for juvenile couplings.

Acknowledgements

REFERENCES CITED

Bedford, G. O. 1978. Biology and ecology of the Phasmatodea. Annu. Rev. Entomol. 23: 125–49.

Cade, W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. Science 190: 1312–3.

Chaplin, S. J. 1973. Reproductive isolation between two sympatric species of *Oncopeltus* (Hemiptera: Lygaeidae) in the tropics. Ann. Entomol. Soc. Am. 66: 997–1000.

Chopard, L. 1938. La biologie des orthopteres. Vol. 20, Encyclopedie Entomologique. Paul Lechevalier, Paris. 541 pp.

Clark, B. 1962. Balanced polymorphism and the diversity of sympatric species. P. 47–70. *In* D. Nichols, ed., Taxonomy and Geography. Syst. Assoc. Publ. 4.

Clark, J. T. 1974. Stick and Leaf Insects. Barry Shurlock and Co., Winchester. 65 pp.

Clausen, C. P. 1940. Entomophagous Insects. McGraw-Hill Book Co. Inc., New York. 688 pp.

Cott, H. B. 1957. Adaptive Coloration in Animals. Methuen and Co., Ltd., London. 508 pp.

Daly, M. 1978. The cost of mating. Am Nat. 112: 771–4.

Downes, J. A. 1978. Feeding and mating in the insectivorous Ceratopogoninae (Diptera). Mem. Entomol. Soc. Can. No. 104.

Edmunds, M. 1974. Defense in Animals. Longman Inc., New York. 357 pp.

Edmunds, M. 1976. The defensive behavior of Ghanaian praying mantids with a discussion of territoriality. Zool. J. Linn. Soc. 58: 1–37.

Eisner, T. 1965. Defensive spray of a phasmid insect. Science 148: 966–8.

Eisner, T. 1970. Chemical defense against predation in arthropods. P. 115–217. *In* E. Sondheimer and J. B. Simeone, eds., Chemical Ecology. Academic Press, New York.

Gangrade, G. A. 1963. A contribution to the biology of *Necroscia sparaxes* Westwood (Phasmidae: Phasmida). Entomologist 96: 83–93.

Gustafson, J. F. 1966. Biological observations on *Timema californica* (Phasmoidea: Phasmidae). Ann. Entomol. Soc. Am. 59: 59–61.

Henry, C. S. 1972. Eggs and repagula of *Ululodes* and *Ascaloptynx* (Neuroptera: Ascalaphidae): a comparative study. Psyche 79: 1–22.

Hetrick, R. 1949. The oviposition of the two striped walkingstick *Anisomorpha buprestoides* (Stoll) (Orthoptera, Phasmidae). Proc. Entomol. Soc. Wash. 51: 103–4.

Jackson, R. R. 1976. Predation as a selection factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Salticidae: Araneas). Psyche 83: 243–5.

Korbott, K. 1961. Observations of the life histories of *Achrophylla tessellata* Gray and *Extatosoma tiaratum* Macleay (Phasmida). Univ. Qd. Pap. Entom. 1: 161–9.

Le Feuvre, W. P. 1939. A phasmid with a spermatophore. Proc. R. Entomol. Soc. London (A) 14:24.

Lloyd, J. E. 1973. Firefly parasites and predators. Coleopt. Bull. 27: 91–106.

Mangold, J. R. 1978. Attraction of *Euphasiopteryx ochracea, Corethrella* spp. and gryllids to broadcast songs of the southern male cricket. Fla. Entomol. 61: 57–61.

Mitchell, W. C., and R. F. L. Mau. 1971. Response of the southern green stink bug and its parasite *Trichopoda pen-* *nipes* to male stink bug pheromones. J. Econ. Entomol. 64: 856–9.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45: 525–7.

Parker, G. A. 1974. Courtship persistence and female guarding as male time investment strategies. Behaviour 48: 157–84.

Robinson, M. H. 1969a. Defenses against visually hunting predators. Evol. Biol. 3: 225–59.

Robinson, M. H. 1969b. The defensive behavior of some orthopteroid insects from Panama. Trans. R. Entomol. Soc. London 121: 281–303.

Robinson, M. H. 1973. The evolution of cryptic postures in insects, with special reference to some New Guinea Tettigoniids (Orthoptera). Psyche 80: 159–65.

Severin, H. H. P. 1911. The life history of the walkingstick *Diapheromera femorata.* J. Econ. Entomol. 4: 307–20.

Sivinski, J. 1977. Factors affecting mating duration in the walkingstick *Diapheromera velii* (Walsh) (Phasmatodea: Heteronemiidae). M. S. Thesis, Univ. of New Mexico.

Sivinski, J. 1978. Intrasexual aggression in the stick insects *Diapheromera veliei* and *D. covillea* and sexual dimorphism in the Phasmatodea. Psyche 85: 395–405.

Tostowaryk, W. 1972. The effect of prey density on the functional response of *Podisus modestus* (Hemiptera: Pentatomidae) to the densities of the sawflies *Neodiprion swainei* and *N. pratti banksianae* (Hymenoptera: Neodiprionidae). Can. Entomol. 104: 61–9.

Walker, T. J. 1964. Experimental demonstration of a cat locating orthopteran prey by the prey's calling song. Fla. Entomol. 47: 163–5.